

# Genetic association of cotton yield with its component traits in derived primitive accessions crossed by elite upland cultivars using the conditional ADAA genetic model

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**Abstract** Boll number, lint percentage, and boll weight are three component traits for lint yield of upland cotton, *Gossypium hirsutum* L. Selecting high yielding lines or hybrids depends on the ability to dissect the genetic relationship of lint yield with these component traits. In this study, 14 day-neutral lines with desirable fiber quality derived from primitive accessions were top crossed with five commercial cultivars. The F<sub>2</sub> populations and parents were grown in one location in 1998 and two locations in 1999 at Mississippi State, MS. The F<sub>3</sub> populations and parents were grown in two locations in 2000. Lint yield and three component traits were measured and analyzed by the ADAA genetic model with the mixed model based conditional approach. Results showed that boll number or boll number with lint percentage or boll weight contributed to the majority of the

phenotypic variance and variance components for lint yield. Boll number was more important than the other two component traits in terms of various genetic effects. The results also showed that the combination of boll number and boll weight greatly increased the contribution to lint yield even though boll weight itself had no significant contribution to lint yield compared to boll number alone. The genetic contribution effects were also predicted due to single component traits or their combinations for parents and crosses. The results revealed that the balanced selection of boll weight and boll number should be considered to obtain high yielding hybrids or pure lines.

**Keywords** Contribution ratio · Conditional genetic model · Cotton yield traits · Upland cotton

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## Abbreviations

ADAA Additive, dominance, additive × additive  
genetic model  
CR Contribution ratio

## Introduction

Cotton, *Gossypium* spp., as one of the most important cultivated crops in the world, is the leading fiber resource for the textile industry. Developing high yielding cotton cultivars with improved fiber traits

and resistance to environmental stress is the primary breeding task nowadays. Research showed that the average coefficients of parentage among 260 cultivars released from 1970 to 1990 was 0.7 (Bowman et al. 1996); however, upon examining pedigrees 236 cases of reselections were found in these 260 cultivars (Bowman et al. 1997; Calhoun et al. 1994, 1997). Such a high rate of reselection in cultivar development is an indication of a narrow genetic base that may result in limited genetic gain and increased vulnerability to stressful environments.

The derived lines from primitive accessions of *G. hirsutum* have been reported to contain useful genetic resources for upland cotton improvement (Percival 1987; Percival and Kohel 1990; Meredith 1990; McCarty and Jenkins 1992; McCarty et al. 1995, 1998a, b; 2004a, b; 2005a, 2006). In order to understand their utility in breeding programs, some derived day-neutral lines have been further investigated in their hybrid forms (Swindle 1993; McCarty et al. 2003, 2004a, b; 2005a). Previous reports showed that more than 50 out of 70 F<sub>2</sub> or F<sub>3</sub> hybrids had improved fiber strength compared to the cultivar Deltapine 50 while remaining high yielding levels comparable to their commercial cultivars in their hybrid forms (McCarty et al. 2003, 2004b).

Boll number, boll weight, and lint percentage are three influential component traits to lint yield in cotton. Worley et al. (1974) reported that bolls per unit of land area were the leading contributor to lint yield. Maintaining a high lint percentage was necessary to ensure high lint yield (Culp and Harrell 1975). Covariance component analyses have shown that lint yield was significantly dependent on each of these three yield components concerning different genetic effects (Wu et al. 1995; Tang et al. 1996; McCarty et al. 1998a).

Correlation analysis, multiple linear regression analysis, and path analysis are three common approaches used to detect the relationship between a target trait and its component traits (Wright 1920; Worley et al. 1974; Culp and Harrell 1975; Bora et al. 1998; Samonte et al. 1998; Cramer and Wehner 2000; Ball et al. 2001). Several other approaches have also been proposed for analyzing a complex trait with multiplicative component traits (Sparnaaij and Bos 1993; Melchinger et al. 1994; Peipho 1995). However, the above approaches are not able to dissect the

relationships between a target trait and its component traits in terms of different genetic effects. The mixed model based conditional approach has been proposed so that complicated genetic relationships between a complex trait and its component traits can be detected (Zhu 1995; Wu et al. 2004, 2006a; Wen and Zhu 2005; Xia et al. 2005). Zhu (1995) reported that bolls per plant contributed to about 45% of the variation in lint yield in terms of additive and additive by environment interaction effects, while 2% of the variation was contributed by dominance and dominance by environment interaction effects. However, Zhu's (1995) approach was based on single variable conditional analysis. Yield components have been reported to be significantly correlated (Wu et al. 1995; Tang et al. 1996; McCarty et al. 1998a), which could greatly complicate the multivariable conditional analysis under a particular genetic model. Thus, a recursive conditional approach with flexibility of genetic model extension was proposed (Wu et al. 2006a). With this recursive approach, multivariate conditional variance components and condition effects can be easily calculated. In addition, the contribution ratios and contribution effects can be determined accordingly (Wu et al. 2004, 2006a). Our previous results showed that boll number or boll number with other component trait(s) was the major contributor to lint yield in terms of genotypic effects (Wu et al. 2004, 2006a). The mixed model based conditional analysis has also been used in tobacco (Xiao et al. 2005).

Additive  $\times$  additive (AA) effects, as one type of epistatic effects, are very important because they can be fixed for pure line selection (Cheverud and Routman 1996; McCarty et al. 2004a) and can be used for hybrid prediction as well (Xu and Zhu 1999; McCarty et al. 2004b). Previous studies have showed the existence of AA effects for yield and yield component traits (Xu and Zhu 1999; McCarty et al. 2004a, b, 2005b; Wu et al. 2006b). In a study conducted by McCarty et al. (2004a, b) genetic variance components and genetic effects for several agronomic and fiber traits were reported while the genetic associations between lint yield and its three component traits have not been determined. In the present study we applied the conditional ADAA genetic model extended from our previous study (Wu et al. 2006a) to further reveal the genetic relationships

between lint yield and its component traits, and thus it is a continuation of our previous studies (McCarty et al. 2004a, b). Conditional variance components, contribution ratios, and contribution effects for different component traits were determined. The results should provide a better understanding of genetic relationship between lint yield and yield component traits and could be applied to lint yield improvement through appropriate indirect selection on one or several component traits.

## Materials and methods

### Plant materials and experimental design

The mating design used for this experiment was a North Carolina Design II (Comstock and Robison 1948). Five cultivars used as female parents were crossed to each of fourteen males in 1997 (McCarty et al. 2003, 2004a, b). The male parents were derived from day-neutral selections from crosses of cultivars with exotic primitive race accessions. Female parents were 1. ‘Deltapine 50’ (DP50), 2. ‘DES119’, 3. ‘Stoneville 474’ (ST474), 4. ‘Deltapine Acala 90’ (DP90), and 5. ‘Sure-Grow 125’ (SG125). The male parents were inbred lines ( $F_6$  lines) and were designated as parents 6 through 19. They were as follows: M75-1(6), M1388-1(7), M1388-2(8), M1388-3(9), M239-1(10), M239-2(11), M239-3(12), M239-4(13), M239-5(14), M239-6(15), M239-7(16), M237-1(17), M237-2(18), and M237-3(19), where, male parents 7 through 9, 10 through 16, and parents 17 through 19 were sister lines selected from  $F_2$  individuals of the same cross. A complete description of how the male parent lines were developed was provided by McCarty et al. (2003).

Crosses and subsequent evaluations were conducted at the Plant Science Research Center, Mississippi State, MS (33.4° N, 88.8° W).  $F_1$  and male parent seed were sent to a winter nursery to produce the  $F_2$  and provide for seed increase. Seed from the 70  $F_2$  hybrids and the 19 parents (5 female cultivars and 14 exotic males) were grown at one and two locations in 1998 and 1999, respectively. Seeds were harvested from the 1999 test and the resulting  $F_3$  populations and parents were grown at two locations in 2000.

The combination of year and location (Loc) was considered as environments (Env) for the purpose of statistical analyses. The environments were as follows: Env 1 = 1998, Loc 1; Env 2 = 1999, Loc 1; Env 3 = 1999, Loc 2; Env 4 = 2000, Loc 1; Env 5 = 2000, Loc 2. The experimental design was a randomized complete block with four replications at each location each year. Plot size for environments 1, 3, and 5 was a single row 12 m in length with row spacing of 0.97 m. Plot size for environments 2 and 4 was a single row 9 m in length with row spacing of 0.97 m. The planting for environment one was a two planted-one skip row pattern; whereas, other environments were planted in a solid row pattern. The stand density for all environments was one plant spaced approximately 10 cm apart. Environments one, three, and five soil type was a Marietta silty clay loam (Fine-loamy, siliceous, active, Fluvaquentic Eutrudepts). Environments two and four soil type was a Marietta loam (Fine-loamy, siliceous, active, fluvaquentic Eutrudepts). Standard production practices were followed at all environments.

A 25-boll, hand-harvested sample was collected from each plot prior to machine harvest. These samples were weighed and ginned on a laboratory 10-saw gin to determine boll weight and lint percentage. The plots were harvested with a mechanical picker, and the seed cotton was weighed and this data was used to calculate yields. Boll number per hectare was calculated by dividing seed cotton yield by boll weight (Tang et al. 1996). Lint yield per hectare was determined by multiplying seed cotton yield by lint percentage.

### Genetic models and analysis methods

Additive-dominance additive  $\times$  additive (ADAA) and  $G \times E$  interaction genetic model was employed for data analysis (Zhu 1994; McCarty et al. 2004a; Wu et al. 2006b).

The mixed linear models were as follows:

Parents:

$$y_{hiik(p)} = \mu + E_h + 2A_i + D_{ii} + 4AA_{ii} + 2AE_{hi} + DE_{hii} + 4AAE_{hii} + B_{k(h)} + e_{hiik} \quad (1)$$

F2:

$$\begin{aligned}
 y_{hijk(F_2)} = & \mu + E_h + (A_i + A_j) + \frac{1}{4}D_{ii} + \frac{1}{4}D_{jj} + \frac{1}{2}D_{ij} \\
 & + (AA_{ii} + AA_{jj} + 2AA_{ij}) \\
 & + (AE_{hi} + AE_{hj}) + \frac{1}{4}DE_{hii} + \frac{1}{4}DE_{hjj} \\
 & + \frac{1}{2}DE_{hij} + (AAE_{hii} + AAE_{hjj} + 2AAE_{hij}) \\
 & + B_{k(h)} + e_{hijk}
 \end{aligned} \quad (2)$$

F3:

$$\begin{aligned}
 y_{hijk(F_3)} = & \mu + E_h + (A_i + A_j) + \frac{3}{8}D_{ii} + \frac{3}{8}D_{jj} + \frac{1}{4}D_{ij} \\
 & + (AA_{ii} + AA_{jj} + 2AA_{ij}) \\
 & + (AE_{hi} + AE_{hj}) + \frac{3}{8}DE_{hii} + \frac{3}{8}DE_{hjj} \\
 & + \frac{1}{4}DE_{hij} + (AAE_{hii} + AAE_{hjj} + 2AAE_{hij}) \\
 & + B_{k(h)} + e_{hijk}
 \end{aligned} \quad (3)$$

Where,

$A_i$  (or  $A_j$ ) is additive effect form parent  $i$  (or  $j$ ),  $A_i$  or  $A_j \sim N(0, \sigma_A^2)$ ;

$D_{ii}$ ,  $D_{jj}$  or  $D_{ij}$  is the dominance effect,  $D_{ii}$ ,  $D_{jj}$  or  $D_{ij} \sim N(0, \sigma_D^2)$ ;

$AA_{ii}$ ,  $AA_{jj}$ , or  $AA_{ij}$  is the additive  $\times$  additive (AA) epistasis effect,  $AA_{ii}$ ,  $AA_{jj}$ , or  $AA_{ij} \sim N(0, \sigma_{AA}^2)$ ;

$AE_{hi}$  (or  $AE_{hj}$ ) is additive by environment interaction effect,  $AE_{hi}$  (or  $AE_{hj}$ )  $\sim N(0, \sigma_{AE}^2)$ ;

$DE_{hii}$ ,  $DE_{hjj}$  or  $DE_{hij}$  is the dominance by environment interaction effect,  $DE_{hii}$ ,  $DE_{hjj}$  or  $DE_{hij} \sim N(0, \sigma_{DE}^2)$ ;

$AAE_{hii}$ ,  $AAE_{hjj}$ , or  $AAE_{hij}$  is the AA by environment interaction effect,  $AAE_{hii}$ ,  $AAE_{hjj}$ , or  $AAE_{hij} \sim N(0, \sigma_{AAE}^2)$ ;

$B_{k(h)}$  is the block effect with  $B_{k(h)} \sim N(0, \sigma_B^2)$ ;

$e_{hijk}$  is the random error with  $e_{hijk} \sim N(0, \sigma_e^2)$ .

With this ADAA model in conjunction with the recursive approach (Wu et al. 2006a) the conditional and unconditional variance components were estimated by MINQUE (1), in which all prior values were set as 1.0 (Zhu 1989). Conditional and unconditional effects were predicted by an adjusted

unbiased prediction (AUP) approach (Zhu 1993). Both unconditional and conditional phenotypic variance ( $V_p$ ) was defined as follows,  $V_p = V_A + V_D + V_{AA} + V_{AE} + V_{DE} + V_{AAE} + V_e$  where,  $V_A = 2\sigma_A^2$  for additive effects,  $V_D = \sigma_D^2$  for dominance effects,  $V_{AA} = 4\sigma_{AA}^2$  for additive  $\times$  additive effects,  $V_{AE} = 2\sigma_{AE}^2$  for additive by environment interaction effects,  $V_{DE} = \sigma_{DE}^2$  for dominance by environment effects,  $V_{AAE} = 4\sigma_{AAE}^2$  for AA by environment interaction effects, and  $V_e = \sigma_e^2$  for random errors. The quantity  $1.0 - V_{P(LYcomponent(s))} / V_{P(LY)}$  is defined as the phenotypic contribution ratio  $CR_{P(component(s) \rightarrow LY)}$  from single or multiple component traits, where  $\sigma_{P(LYcomponent(s))}^2$  is the phenotypic conditional variance (obtained in this study) and  $\sigma_{P(LY)}^2$  the unconditional variance (obtained in previous study, McCarty et al. 2004a) for lint yield, respectively. The quantity  $1.0 - \sigma_{u(LYcomponent(s))}^2 / \sigma_{u(LY)}^2$  is defined as the contribution ratio  $CR_{u(component(s) \rightarrow LY)}$  from single or multiple component traits for the  $u$ -th random effect, where  $\sigma_{u(LYcomponent(s))}^2$  is the  $u$ -th conditional variance component and  $\sigma_{u(LY)}^2$  the  $u$ -th unconditional variance component for lint yield (Zhu 1995; Wu et al. 2004, 2006a). The vector  $\mathbf{e}_{u(LY)} - \mathbf{e}_{u(LYcomponent(s))}$  is defined as the  $u$ -th contribution effect vector,  $\mathbf{e}_{u(component(s) \rightarrow LY)}$ , from single or joint yield components to lint yield, where  $\mathbf{e}_{u(LY)}$  is the  $u$ -th effect vector for lint yield and  $\mathbf{e}_{u(LYcomponent(s))}$  is the  $u$ -th conditional effect vector for lint yield given one or more component traits (Wu et al. 2006a). Resampling (the jackknifing) method was applied to calculate the standard error (SE) for each parameter by removal of each block within environment (20 blocks in total) (Miller 1974). An approximate  $t$ -test (degrees of freedom = 19) was used to detect the significance of each parameter and 95% confidence intervals were used to test the difference among parameters. All data analyses were conducted using a self-written program in C++ (Wu et al. 2004, 2006a).

## Results

Phenotypic correlations among lint yield and yield components by generations

Phenotypic correlations among lint yield and three yield components are summarized for parents,  $F_2$

**Table 1** Phenotypic correlations among lint yield (LY) and yield components, lint percentage (LP), boll weight (BW), and boll number (BN), by generations (parent,  $F_2$ , and  $F_3$ )

	Parent		
	BW	BN	LY
LP	0.23**	0.30**	0.58**
BW		0.10	0.34**
BN			0.92**
	$F_2$		
	BW	BN	LY
LP	−0.32**	0.09	0.11
BW		−0.25**	−0.11
BN			0.98**
	$F_3$		
	BW	BN	LY
LP	−0.46**	−0.30**	−0.24**
BW		0.39**	0.59**
BN			0.96**

\*, significant at  $\leq 0.05$ \*\*, significant at  $\leq 0.01$ 

populations, and  $F_3$  populations, respectively (Table 1). Lint percentage for parents had significant and positive correlations with boll weight (0.23), boll number (0.30), and lint yield (0.58) (Table 1). Lint yield were positively correlated with boll weight (0.34) and boll number (0.92). Lint percentage for  $F_2$  populations was only negatively correlated with boll weight (−0.32) (Table 1). Boll number was negatively correlated with boll weight (−0.25) and positively correlated with lint yield (0.98). In contrast to parents, lint percentage for  $F_3$  populations was negatively correlated with three traits, boll weight, boll number, and lint yield (−0.46, −0.30, and −0.24, respectively) (Table 1). Boll weight was positively correlated with boll number (0.39) and lint yield (0.59) and boll number was highly correlated with lint yield (0.96) for  $F_3$  populations.

In summary, lint yield was highly correlated with boll number for parental lines,  $F_2$  populations, and  $F_3$  populations, indicating that lint yield was mainly determined by boll number. On the other hand, the correlation structures among these agronomic traits except correlation between boll number and lint yield differed among generations. Thus, the results indicated that other genetic factors might also be responsible for these traits in addition to additive effects (McCarty et al. 2004a).

### Contribution ratios due to yield components

Variance component proportions for yield and yield components were reported previously with the ADAA model (McCarty et al. 2004a). The contributions to the phenotypic variance for lint yield were 6.1%, 25.4%, 3.0%, 3.2%, 31.4%, and 2.7% due to additive effects (A), dominance effects (D), additive  $\times$  additive (AA) effects, additive  $\times$  environment interaction (AE) effects, dominance  $\times$  environment interaction (DE) effects, AA  $\times$  environment interaction (AAE) effects, respectively, indicating that dominance effects and DE effects were primarily responsible for the phenotypic variance in lint yield (McCarty et al. 2004a). In this study, the conditional variance components for lint yield given one or more component traits (data not presented) were estimated and the contribution ratios were calculated according to the conditional ADAA model (Table 2). Sixty nine percent, 38%, 23%, and 34% of the variance components for additive (A), dominance (D), A  $\times$  environment (AE), and AA  $\times$  environment effects in lint yield were contributed by lint percentage. Since additive effects had small contribution (6.1%) to lint yield, even though large percentage of additive variance for lint yield (69%) was due to lint percentage, small contribution to phenotypic variance (19%) was due to this component trait. Twenty four percent of AA variance in lint yield was accounted for by boll weight. Boll number had a large contribution to phenotypic variance (81%) as did all variance components (50%, 86%, 80%, 69%, 84%, 66%, and 85%) regarding the effects of A, D, AA, AE, dominance  $\times$  environment (DE), AAE, and residual for lint yield. Additive and dominance variances (68% and 34%, respectively) for lint yield contributed by both lint percentage and boll weight were similar to those by lint percentage alone. However, variances for AA, AE, and AAE effects (37%, 36%, and 100%, respectively) in lint yield contributed by both lint percentage and boll weight were higher than those by lint percentage alone. Seventy eight percent, 94%, 78%, 77%, 85%, 85%, and 72% for variances of additive, dominance, AA, AE, DE, and AAE effect in lint yield were contributed by both lint percentage and boll number. Combination of boll number and boll weight made numerically more than 80% of contributions for each of variance components (86%, 100%, 92%, 87%,



**Table 2** Contribution ratios (CR) with their standard errors due to yield component traits and their combinations in terms of additive effects, dominance effects, AA effects, and their G × E interaction effects

CR <sup>a</sup>	LP → LY <sup>b</sup>	BW → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
CR <sub>A</sub>	0.69 ± 0.09	0.00 ± 0.07	0.50 ± 0.07	0.68 ± 0.09	0.78 ± 0.09	0.86 ± 0.08	1.00 ± 0.00
CR <sub>D</sub>	0.38 ± 0.09	0.06 ± 0.10	0.86 ± 0.09	0.34 ± 0.09	0.94 ± 0.10	1.00 ± 0.00	1.00 ± 0.00
CR <sub>AA</sub>	0.10 ± 0.10	0.24 ± 0.10	0.80 ± 0.10	0.37 ± 0.10	0.78 ± 0.10	0.92 ± 0.09	0.93 ± 0.10
CR <sub>AE</sub>	0.23 ± 0.10	0.16 ± 0.10	0.69 ± 0.10	0.36 ± 0.10	0.77 ± 0.10	0.87 ± 0.10	0.89 ± 0.11
CR <sub>DE</sub>	0.10 ± 0.10	0.04 ± 0.11	0.84 ± 0.08	0.12 ± 0.10	0.85 ± 0.09	0.93 ± 0.09	0.94 ± 0.10
CR <sub>AAE</sub>	0.34 ± 0.09	0.14 ± 0.09	0.66 ± 0.09	1.00 ± 0.00	0.72 ± 0.09	1.00 ± 0.00	1.00 ± 0.00
CR <sub>e</sub>	0.01 ± 0.01	0.11 ± 0.02	0.85 ± 0.02	0.11 ± 0.02	0.86 ± 0.02	0.96 ± 0.02	0.96 ± 0.02
CR <sub>P</sub>	0.19 ± 0.04	0.08 ± 0.06	0.81 ± 0.03	0.27 ± 0.05	0.86 ± 0.02	0.95 ± 0.01	0.97 ± 0.01

<sup>a</sup> CR<sub>A</sub>, CR<sub>D</sub>, CR<sub>AA</sub>, CR<sub>AE</sub>, CR<sub>DE</sub>, and CR<sub>AAE</sub> are contribution ratios for additive effects, dominance effects, additive by additive interaction (AA) effects, additive × environment interaction effects, dominance × environment interaction effects, and AA × environment interaction effects, respectively. CR<sub>e</sub> and CR<sub>P</sub> are residual and phenotypic contribution ratios, respectively

<sup>b</sup> LY = lint yield, LP = lint percentage, BW = boll weight, BN = boll number

93%, and 100% for variances of additive, dominance, AA, AE, DE, and AAE effects, respectively). Three yield component traits made numerically more than 90% contributions to all variance components except for that of AE effects (89%) in lint yield.

In summary, boll number or boll number with other yield components contributed to the majority of phenotypic variance and variance components in lint yield, indicating that boll number played a more important role for lint yield than the other two component traits, lint percentage and boll weight. Noticeably, the combination of boll number and boll weight made larger contributions to lint yield than the combination of boll number and lint percentage even though lint percentage was more important than boll weight in determination of lint yield in this study. Similar results were also reported in our previous studies (Wu et al. 2004, 2006a). Therefore, balanced selection of boll weight and boll number should be applied to obtain high yielding pure lines. Since additive effects had small contribution to lint yield, small contribution ratio (up to 6.1%) to the phenotypic variance for lint yield due to one or more component traits would be expected.

### Contribution effects

Contribution ratios help us to determine the importance of each component trait or each combination of component traits contributed to lint yield. Breeders may also be interested in which trait or trait combination that is important for specific parents or crosses. Therefore, various types of genetic contribution effects to lint yield were predicted in this study. These genetic contribution effects from yield component(s) to lint yield could be used for indirect selection for high-yielding pure lines (additive contribution effects and AA contribution effects) and/or hybrids (dominance contribution effects and AA contribution effects) and they are summarized in Tables 3–5.

### Additive contribution effects

Additive effects for a quantitative trait can be considered as general combining ability effects, which can be used for pure line selection. Thus,

**Table 3** Additive effects for lint yield (kg ha<sup>-1</sup>, first column) and additive contribution effects to lint yield (kg ha<sup>-1</sup>, the remaining columns)

Parents	LY <sup>a</sup>	LP → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
1. DP50	71.9**	28.4	48.0**	34.7*	39.2*	79.7**	71.9**
2. DES119	115.1**	85.8**	56.7	92.4**	92.0**	85.8**	115.1**
3. ST474	73.5**	74.3**	18.5	74.1**	66.9**	28.7*	73.5**
4. DP90	25.7	33.7**	-21.8	41.1**	17.4	-3.6	25.7
5. SG125	109.9**	72.3**	60.1**	76.8**	83.9**	91.4**	109.9**
6. M75-1	18.5	-14.8	57.4**	-24.1	21.2	30.9*	18.5*
7. M1388-1	-11.8	-11.2*	-1.6	-16.5*	-9.4	-13.4	-11.8
8. M1388-2	-45.0**	-27.0**	-18.3	-30.3**	-29.3*	-38.4**	-45.0**
9. M1388-3	-44.5**	-10.6	52.0**	-35.2**	29.4*	-35.1**	-44.5**
10. M239-1	-19.1	-17.3*	-38.3*	-8.5	-36.8*	-6.2	-19.1
11. M239-2	-40.2**	-40.7**	-25.9*	-36.3**	-45.6**	-20.6	-40.2**
12. M239-3	-49.1**	-37.9**	-37.2*	-35.9**	-48.7**	-37.1*	-49.1**
13. M239-4	-47.2**	-50.4**	-65.6**	-33.3**	-78.0**	-13.0	-47.2**
14. M239-5	-7.4	-24.2*	9.4	-25.4*	-13.5	6.9	-7.4
15. M239-6	-7.8	-9.4	-17.5	-7.6	-19.8	-9.9	-7.8
16. M239-7	-3.9	-35.9*	9.0	-33.9*	-22.8*	18.8*	-3.9
17. M237-1	-39.9**	-31.3**	10.7	-45.2**	-16.5	-29.4**	-39.9**
18. M237-2	-43.6**	6.8	-25.1*	-0.6	-6.9	-62.7**	-43.6**
19. M237-3	-49.2*	12.5	-71.1**	16.8	-22.8	-73.1**	-49.2**

\*, significant at  $\leq 0.05$ ; \*\*, significant at  $\leq 0.01$ <sup>a</sup> Additive effects for lint yield are listed in the first column, additive contribution effects to lint yield due to each component trait or combination of component traits are listed in the second to sixth columns

additive contribution effects can also be considered as indirect general combining ability effects, which can be used for pure line selection of a target trait. The correlations between predicted additive effects for lint yield and additive contribution effects to lint yield were estimated. Except for additive contribution effects due to boll weight, additive effects for lint yield had significant and positive correlations with additive contribution effects due to each single component trait or each combination of these component traits, showing that the squared correlation coefficients were very close to the additive contribution ratios and thus indicating the consistence of additive contribution ratios and additive contribution effects.

P<sub>2</sub> (parent 2) to P<sub>5</sub> (parent 5) had positive additive contribution effects on lint yield due to lint percentage alone, while P<sub>7</sub>, P<sub>8</sub>, P<sub>10</sub>, P<sub>11</sub>–P<sub>14</sub>, P<sub>16</sub>, and P<sub>17</sub> had significant negative additive contribution effects on lint yield due to lint percentage (Table 3). Previous reports showed that P<sub>2</sub>–P<sub>4</sub> had very positive additive

effects on lint percentage while P<sub>7</sub>, P<sub>8</sub>, P<sub>10</sub>–P<sub>14</sub>, and P<sub>16</sub>–P<sub>17</sub> had negative additive effects on lint percentage (McCarty et al. 2004b). P<sub>1</sub>, P<sub>5</sub>, P<sub>6</sub>, and P<sub>9</sub> had positive and significant additive contribution effects while P<sub>10</sub>–P<sub>13</sub>, P<sub>18</sub>, and P<sub>19</sub> had negative additive contribution effects on lint yield due to boll number alone. Additive contribution effects for lint yield due to boll weight were not detected (therefore they are not included in Table 3), indicating that boll weight was not responsible for the additive variance for lint yield in this study. Small genotypic contribution effects on lint yield due to boll weight were also reported previously (Wu et al. 2004, 2006a). Additive contribution effects on lint yield due to lint percentage and boll weight were positive and significant for all female parents, P<sub>1</sub>–P<sub>5</sub>, showing a similar pattern with the additive contribution effects due to lint percentage alone (with correlation coefficient of 0.98). Negative additive contribution effects on lint yield due to lint percentage and boll weight were significantly detected for P<sub>7</sub>–P<sub>9</sub>, P<sub>11</sub>–P<sub>14</sub>, and

**Table 4** Dominance effects for lint yield ( $\text{kg ha}^{-1}$ , first column) and dominance contribution effects to lint yield ( $\text{kg ha}^{-1}$ , the remaining columns)

Cross <sup>a</sup>	LY <sup>b</sup>	LP $\rightarrow$ LY	BW $\rightarrow$ LY	BN $\rightarrow$ LY	LP & BW $\rightarrow$ LY	LP & BN $\rightarrow$ LY	BW & BN $\rightarrow$ LY	LP, BW & BN $\rightarrow$ LY
1 $\times$ 1	-137.5	-57.5 <sup>+</sup>	-102.7*	-111.0	-79.0	-131.7	-137.5	-137.5
2 $\times$ 2	-147.6	23.6	43.8	-241.2	122.3*	-171.2	-147.6	-147.6
3 $\times$ 3	-220.9**	-19.3	-101.1	-179.5*	-26.9	-172.7	-220.9*	-220.9**
4 $\times$ 4	-52.0	-2.6	-69.2*	-75.7	-13.3	-67.0	-52.0	-52.0
5 $\times$ 5	50.6	72.3 <sup>+</sup>	-31.4	-1.5	86.2 <sup>+</sup>	44.7	50.6	50.6
6 $\times$ 6	-299.7**	-214.5	-2.8	-243.2*	-192.3*	-308.2**	-299.7**	-299.7**
7 $\times$ 7	-27.0	-67.7*	18.7	-5.2	-56.2 <sup>+</sup>	-35.0	-27.0	-27.0
8 $\times$ 8	-220.9**	-102.0**	-48.5	-143.9	-114.3*	-181.6	-220.9**	-220.9*
9 $\times$ 9	-301.6**	-56.0	-23.1	-257.4**	-56.2	-264.3*	-301.6**	-301.6**
10 $\times$ 10	-171.4*	-146.0**	-50.9	-102.2	-151.0**	-144.5	-171.4*	-171.4
11 $\times$ 11	-233.5**	-181.1**	-64.1	-134.3	-192.6**	-195.5	-233.5**	-233.5*
12 $\times$ 12	-186.7**	-155.0**	-38.4	-119.2	-160.5**	-169.1*	-186.7*	-186.7*
13 $\times$ 13	-280.9**	-99.3**	-105.7*	-189.7*	-130.4*	-225.7*	-280.9**	-280.9**
14 $\times$ 14	-317.6**	-118.7*	3.8	-278.5*	-68.8	-305.2*	-317.6**	-317.6**
15 $\times$ 15	-83.8	-80.1**	-67.1	-4.3	-98.8*	-46.6	-83.8	-83.8
16 $\times$ 16	-63.1	-94.4**	-25.0	-10.6	-111.3**	-53.7	-63.1	-63.1
17 $\times$ 17	-270.2**	-138.5**	49.1	-243.3*	-81.8	-284.3**	-270.2**	-270.2**
18 $\times$ 18	-244.6**	-145.6**	-61.4	-144.8	-160.0**	-185.9	-244.6*	-244.6*
19 $\times$ 19	-73.2	-46.9**	-49.8	-43.6	-68.3*	-30.7	-73.2	-73.2
1 $\times$ 6	163.2*	70.9*	-53.0	221.8**	21.4	193.3*	163.2	163.2*
1 $\times$ 7	-130.7*	-21.0	-35.7	-103.2	-44.0	-113.4	-130.7*	-130.7*
1 $\times$ 8	198.7**	46.4	84.7**	108.6	86.5**	134.3	198.7**	198.7**
1 $\times$ 9	46.5	10.4	0.5	87.4	-6.6	68.2	46.5	46.5
1 $\times$ 10	-101.3	7.1	83.2*	-157.6**	68.3	-130.9*	-101.3*	-101.3
1 $\times$ 11	141.5**	35.4	64.3	92.4	58.0	105.7	141.5*	141.5*
1 $\times$ 12	-90.4	13.4	16.4	-104.9	39.0	-86.4	-90.4	-90.4
1 $\times$ 13	-5.7	9.5	9.6	-25.0	15.7	-16.3	-5.7	-5.7
1 $\times$ 14	80.6	7.3	-25.3	121.9	-33.5	100.1	80.6	80.6
1 $\times$ 15	126.8	-4.1	58.7*	68.5	10.5	72.4	126.8	126.8
1 $\times$ 16	-100.1	-1.0	4.5	-82.2	8.9	-87.5	-100.1	-100.1
1 $\times$ 17	75.5	8.7	-31.9	122.3	-27.2	115.1	75.5	75.5
1 $\times$ 18	179.3*	73.3**	4.7	141.2	52.9	148.1	179.3*	179.3*
1 $\times$ 19	85.0	14.5	44.6*	32.2	35.4	48.3	85.0	85.0
2 $\times$ 6	96.4	49.6*	-3.0	102.9	33.7	92.4	96.4	96.4
2 $\times$ 7	137.7	56.5*	-30.5	140.6*	17.9	148.4	137.7	137.7
2 $\times$ 8	93.3*	-15.9	-4.8	115.2*	-29.4	94.3	93.3*	93.3*
2 $\times$ 9	159.6**	29.5	-21.5	226.3**	-4.8	192.4**	159.6*	159.6**
2 $\times$ 10	170.2*	38.7	26.0	131.9	25.3	135.0	170.2*	170.2*
2 $\times$ 11	86.8	75.3**	-66.1	104.3	9.2	99.4	86.8	86.8
2 $\times$ 12	0.1	19.5	-29.1	12.7	-18.2	12.3	0.1	0.1
2 $\times$ 13	165.3**	61.7	109.4**	38.3	125.8**	83.4	165.3**	165.3*
2 $\times$ 14	136.7	48.6	-5.7	113.8	30.4	115.9	136.7	136.7
2 $\times$ 15	-51.8	-46.8	-10.6	-16.1	-54.2	-31.5	-51.8	-51.8



**Table 4** continued

Cross <sup>a</sup>	LY <sup>b</sup>	LP → LY	BW → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
2 × 16	73.0	−4.2	−11.4	70.1	−28.7	50.5	73.0	73.0
2 × 17	31.0	18.8	−25.5	47.2	−19.0	34.9	31.0	31.0
2 × 18	75.4	94.9*	14.1	36.1	96.5**	76.8	75.4	75.4
2 × 19	−203.5*	14.0	21.0	−206.3*	68.8	−167.6	−203.5*	−203.5*
3 × 6	124.1	104.2**	22.4	69.4	103.8**	99.5	124.1	124.1
3 × 7	110.9	34.5	21.0	84.7	36.7	93.0	110.9	110.9
3 × 8	7.8	−20.6	13.6	2.9	−15.4	−3.4	7.8	7.8
3 × 9	61.8	−14.5	−50.3*	162.9*	−50.3	122.5	61.8	61.8
3 × 10	13.5	79.5*	−49.2*	21.3	46.9	57.9	13.5	13.5
3 × 11	136.5	24.8	50.6	90.8	36.5	101.3	136.5	136.5
3 × 12	109.2*	60.8**	66.5**	42.7	94.8**	72.7	109.2*	109.2*
3 × 13	165.9	24.5	67.7	89.5	41.6	107.9	165.9	165.9
3 × 14	95.8	1.5	29.5	68.0	−6.4	64.4	95.8	95.8
3 × 15	1.9	36.1	31.5	−64.6	58.8	−35.3	1.9	1.9
3 × 16	−57.7	11.0	23.7	−64.5	32.5	−43.5	−57.7	−57.7
3 × 17	125.1*	43.8	−64.0*	156.7*	−20.5	151.1*	125.1*	125.1*
3 × 18	−103.2	−12.2	12.9	−99.5	13.3	−95.5	−103.2	−103.2
3 × 19	78.7	83.4*	53.6	2.0	116.5*	61.3	78.7	78.7
4 × 6	41.7	−7.0	−2.6	76.4	−19.0	57.4	41.7	41.7
4 × 7	−81.3	−5.4	6.6	−90.0	12.3	−69.8	−81.3	−81.3
4 × 8	−41.3	6.3	−19.6	−38.6	2.3	−25.1	−41.3	−41.3
4 × 9	134.5	32.2	−34.6	183.1	−6.5	167.9	134.5	134.5
4 × 10	99.9	35.6	110.2*	1.3	100.8*	34.3	99.9	99.9
4 × 11	−115.2	5.0	51.5	−145.1*	54.3	−118.8	−115.2	−115.2
4 × 12	−130.3	−39.7	7.6	−96.6	−17.3	−89.4	−130.3	−130.3
4 × 13	−6.9	−15.8	83.0*	−60.0	45.4	−45.6	−6.9	−6.9
4 × 14	−0.5	−38.4	−24.1	39.4	−68.5	18.2	−0.5	−0.5
4 × 15	97.3	64.3**	26.2	52.5	58.8	76.2	97.3	97.3
4 × 16	124.1	−9.1	40.0	62.4	3.2	59.2	124.1	124.1
4 × 17	29.5	−6.6	−40.1	75.2	−36.4	59.5	29.5	29.5
4 × 18	92.0	97.5**	21.2	50.6	104.3**	97.9	92.0	92.0
4 × 19	13.3	76.4*	−9.8	−3.0	75.8*	34.5	13.3	13.3
5 × 6	264.9*	126.7**	−39.7	263.0*	61.2	263.7*	264.9*	264.9*
5 × 7	−51.8	−0.7	−19.0	−47.4	−4.2	−49.4	−51.8	−51.8
5 × 8	−63.1	33.0	−5.0	−29.5	39.3	−11.1	−63.1	−63.1
5 × 9	−65.9	0.3	−38.4	−9.6	−16.9	−20.6	−65.9	−65.9
5 × 10	49.3	13.9	1.0	17.5	11.0	22.7	49.3	49.3
5 × 11	−13.9	−12.9	37.8	−45.9	0.8	−49.2	−13.9	−13.9
5 × 12	190.4*	40.6	31.9	139.3	29.1	137.3	190.4*	190.4*
5 × 13	−28.3	−159.9	60.5	−11.1	−131.1*	−61.8	−28.3	−28.3
5 × 14	280.9**	78.8	6.3	240.5*	46.7	245.7*	280.9**	280.9*
5 × 15	−49.3	47.0	46.8	−117.0	80.2	−82.8	−49.3	−49.3
5 × 16	66.4	−22.7	4.7	67.2	−24.5	32.9	66.4	66.4
5 × 17	56.3	20.9	−18.2	74.3	0.4	72.8	56.3	56.3

**Table 4** continued

Cross <sup>a</sup>	LY <sup>b</sup>	LP → LY	BW → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
5 × 18	-3.9	86.5	3.1	-13.4	86.8*	20.8	-3.9	-3.9
5 × 19	-106.6	17.2	20.9	-104.9	39.4	-83.2	-106.6	-106.6

\*, significant at  $\leq 0.05$ ; \*\*, significant at  $\leq 0.01$

<sup>a</sup> Parents for cross are given in Table 3

<sup>b</sup> Dominance effects for lint yield are given in the first column and dominance contribution effects to lint yield due to each component trait or combination of component traits are given in the second to seventh columns.

**Table 5** AA effects for lint yield (kg ha<sup>-1</sup>, the first column)) and AA contribution effects to lint yield (kg ha<sup>-1</sup>, the remaining columns)

Cross <sup>a</sup>	LY <sup>b</sup>	LP → LY	BW → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
1 × 1	10.2	8.3*	2.1	-7.0	15.8*	-6.3	1.3	3.6
2 × 2	-34.1	38.5**	-25.5*	-22.8	2.0	1.3	-43.9	-37.3
3 × 3	-4.08	32.8**	-6.1	-19.0*	34.3	-0.6	-25.1**	2.0
4 × 4	6.1	18.7*	-13.0	-2.8	7.0	10.7	-18.0*	-5.6
5 × 5	-17.8	37.3**	-8.3	-29.3*	29.9	-12.1	-32.7*	-16.4
6 × 6	-59.4**	-34.6*	-9.9	-29.8	-46.0**	-45.4*	-41.1	-60.9**
7 × 7	-24.6	-15.2*	-1.2	-15.7	-15.5*	-22.8	-21.4	-24.2
8 × 8	-46.4*	-17.3	-12.9	-21.2	-29.5*	-24.6	-40.8	-46.4*
9 × 9	-60.5**	-4.9	1.0	-43.4	-3.8	-44.6	-57.2*	-55.1*
10 × 10	-58.8*	-18.3	-13.0	-41.4	-29.2	-43.4	-51.1*	-54.6*
11 × 11	-63.6*	-28.2	-11.7	-42.5	-36.5*	-51.2*	-54.5*	-62.8*
12 × 12	-46.9*	-28.2*	-7.3	-30.1	-33.0*	-38.5	-40.1*	-46.0*
13 × 13	-43.9*	-17.8	-17.7	-25.9	-29.7*	-29.6	-38.2*	-44.0*
14 × 14	-46.1*	-13.6	-8.7	-27.8	-23.0	-33.4	-37.6	-44.1*
15 × 15	-31.1**	-13.7	-14.1*	-13.0	-23.9**	-16.8	-28.7**	-32.8**
16 × 16	-59.5*	-23.0	-5.9	-38.9	-28.8	-49.9	-41.8	-53.3*
17 × 17	-43.2*	-22.4*	6.5	-29.2	-16.4	-39.3*	-28.0	-31.3
18 × 18	-24.9	-18.8*	-11.2	-1.8	-29.3*	-1.9	-23.3	-24.3
19 × 19	-52.2*	-0.6	-15.0	-32.6*	-19.3	-17.9	-53.9*	-46.2*
1 × 6	27.7*	9.9	-13.4	34.5*	1.3	31.5*	20.2	21.3
1 × 7	-7.5	-0.5	-9.9	3.5	-11.6*	4.3	-5.3	-10.3
1 × 8	6.8	-0.2	-0.9	4.2	-7.3	1.6	4.4	-1.7
1 × 9	-8.7	4.1	-8.7	10.2	-6.3	11.5	-4.7	-5.0
1 × 10	3.1	0.2	23.0**	-14.0	23.8*	-15.5*	16.2*	21.9**
1 × 11	-2.2	-2.9	-0.1	-0.2	-6.7	-3.1	3.2	-2.5
1 × 12	-3.4	6.4*	-3.5	-2.6	2.5	-0.7	-3.3	-2.1
1 × 13	-14.4	-3.3	8.4	-16.1	4.0	-17.7	1.1	-2.4
1 × 14	18.4	-8.5*	0.5	23.7*	-6.0	16.6	27.4*	18.7
1 × 15	31.1*	-11.4*	14.6*	13.1	2.8	3.4	29.6**	25.6*
1 × 16	-2.9	-0.9	-2.0	5.7	-3.9	4.2	8.4	3.1
1 × 17	6.3	-6.9*	-1.2	12.1	-7.9	6.5	10.0	2.8
1 × 18	18.0	8.0	-6.8	18.3	0.7	20.4*	5.9	7.9

**Table 5** continued

Cross <sup>a</sup>	LY <sup>b</sup>	LP → LY	BW → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
1 × 19	25.2**	2.5	10.7*	7.1	14.1**	8.0	15.4	22.8**
2 × 6	33.6**	2.0	5.0	29.2	8.7	24.6	33.3*	31.2*
2 × 7	16.7	4.4	−9.0	20.0	−6.8	21.1	10.2	5.2
2 × 8	17.6	−4.8	13.0	5.7	13.9*	0.7	19.2	23.9
2 × 9	13.5	1.9	−10.2	36.0**	−11.3	36.8**	21.6*	17.1*
2 × 10	32.8	−8.1	12.0	18.9	3.9	12.9	36.0	31.6
2 × 11	27.2	7.2	−1.0	19.8	12.2	19.6	16.2	19.1
2 × 12	27.3*	−3.1	7.4	17.6*	6.9	14.1	24.9*	23.3*
2 × 13	18.0	3.8	24.0*	−13.6	27.9*	−16.7	18.6	23.2
2 × 14	34.0	3.3	10.3	13.1	19.7*	8.2	22.5	25.4
2 × 15	−12.2	−2.4	10.8	−21.6*	12.1	−22.4*	−5.3	−0.8
2 × 16	36.6	−11.5*	−0.1	32.0	−9.6	23.1	33.7	23.7
2 × 17	10.8	−1.8	−2.5	16.0	−4.8	14.0	10.5	5.2
2 × 18	17.3	18.6*	8.3	3.5	26.8*	10.5	7.4	17.6
2 × 19	−27.0**	24.7**	−0.6	−29.8**	22.7	−12.0	−30.5**	−13.4
3 × 6	36.6*	10.8	7.2	24.2*	17.8 <sup>+</sup>	22.9	26.9*	27.3*
3 × 7	5.9	1.3	4.0	5.0	0.2	6.2	9.6	5.8
3 × 8	17.6	−7.6**	10.0	7.2	4.4	3.5	16.2	18.2
3 × 9	−3.5	4.1	−17.6*	23.7*	−15.0	28.1*	−0.2	−1.3
3 × 10	−6.0	17.0**	−6.8	−6.2	8.6	3.5	−10.8	−7.8
3 × 11	18.6	−6.6	13.3	7.8	6.8	3.0	23.8	22.5
3 × 12	13.2	3.2	7.6	4.0	7.1	5.0	12.5	13.5
3 × 13	12.6	−5.0	0.1	3.8	−8.7	1.0	8.0	1.1
3 × 14	13.3	−10.4*	5.9	14.7	−7.5	9.7	21.4 <sup>+</sup>	11.0
3 × 15	−8.1	12.3**	−14.4*	−4.7	−8.5	3.5	−19.3	−20.5
3 × 16	8.1	2.8	11.6**	0.7	13.6*	0.7	14.2	15.0
3 × 17	14.0	3.1	−12.7	22.6	−10.1	22.9	3.5	−1.9
3 × 18	−11.0	11.0**	2.4	−16.1*	17.1	−8.0	−17.7*	−4.6
3 × 19	13.3	15.5**	10.5	−6.2	24.4*	3.4	4.0	16.9
4 × 6	13.3	−8.3**	6.6	15.8	−0.7	10.2	22.6*	18.8
4 × 7	−4.3	5.2*	0.8	−8.6	5.5	−5.3	−7.7	−4.6
4 × 8	−7.7	7.3**	−5.9	−5.5	1.3	−0.8	−12.2	−8.6
4 × 9	31.1**	2.0	−12.4	46.8**	−11.2	47.2**	25.8	23.5
4 × 10	19.3	−2.2	17.8*	2.2	12.3	0.8	24.3*	26.9*
4 × 11	2.1	0.7	9.4	−3.8	8.5	−2.2	8.3	11.9
4 × 12	−31.2	0.4	7.4	−31.2*	8.7	−27.2*	−19.0	−10.7
4 × 13	−2.1	−6.9	13.5*	−14.4*	4.1	−16.6*	5.9	6.4
4 × 14	−24.4	−4.2	−2.3	−15.0	−7.1	−14.7	−14.4	−15.9
4 × 15	7.8	5.5*	9.4	−1.5	15.0*	0.5	8.6	11.4
4 × 16	32.9	−12.1	5.9	16.7	−3.2	7.0	22.4	17.0
4 × 17	−9.8	2.4	−12.8*	2.4	−10.5*	4.2	−12.7	−13.5
4 × 18	−16.6*	20.6**	4.8	−25.4**	24.3	−14.0	−23.5**	−9.0
4 × 19	14.5	18.3**	−1.2	0.5	20.9	11.6	−3.9	9.8

**Table 5** continued

Cross <sup>a</sup>	LY <sup>b</sup>	LP → LY	BW → LY	BN → LY	LP & BW → LY	LP & BN → LY	BW & BN → LY	LP, BW & BN → LY
5 × 6	40.3**	10.5	−5.8	41.7**	4.0	39.1**	32.5*	26.0*
5 × 7	19.2	4.0	8.0	5.7	16.0*	4.4	14.0	16.9
5 × 8	−16.9	11.2**	−3.2	−9.5	5.6	−2.8	−10.8	−8.0
5 × 9	20.3	5.2	−5.0	30.6*	1.1	31.6*	19.2	19.9
5 × 10	39.1**	−1.3	−0.8	27.0	0.2	23.8	28.5	25.5
5 × 11	18.4	−11.0**	7.6	17.5	−4.8	12.1	26.8*	20.3*
5 × 12	12.3	−2.4	−2.4	12.7	−7.4	10.6	9.0	2.7
5 × 13	−1.2	−33.3**	19.9*	−7.5	−11.3	−21.6*	24.3	17.8
5 × 14	37.3	−1.1	−1.1	28.2	−2.7	22.1	28.1	20.2
5 × 15	31.9*	3.4	11.6	16.4	12.9	15.6	28.6*	26.0
5 × 16	38.2*	−11.6	−1.2	33.9	−10.9	24.3	36.1*	26.9
5 × 17	0.6	2.9	−9.0	8.2	−9.5	8.6	−2.8	−7.6
5 × 18	−26.6	22.2**	−2.8	−20.7	13.6	−7.1	−25.7	−18.8
5 × 19	−1.4	11.1**	16.4	−16.1	28.9*	−7.7	3.4	18.9*

\*, significant at  $\leq 0.05$ ; \*\*, significant at  $\leq 0.01$

<sup>a</sup> Parents for cross are given in Table 3

<sup>b</sup> AA effects for lint yield were listed in the first column and AA contribution effects to lint yield due to each component trait or combination of component traits were listed in the second to seventh columns

P<sub>16</sub>–P<sub>17</sub>. Positive additive contribution effects on lint yield due to lint percentage and boll number were detected for P<sub>1</sub>–P<sub>3</sub> and P<sub>5</sub>, while negative effects were detected for P<sub>8</sub>–P<sub>13</sub> and P<sub>16</sub> due to the same two component traits. Positive additive contribution effects on lint yield were detected for P<sub>1</sub>–P<sub>3</sub>, P<sub>5</sub>, P<sub>6</sub>, and P<sub>16</sub> due to boll number and boll weight, while negative effects were detected for P<sub>8</sub>, P<sub>9</sub>, P<sub>12</sub>, and P<sub>17</sub>–P<sub>19</sub> due to the same two component traits. Positive additive contribution effects were detected for P<sub>1</sub>–P<sub>3</sub>, P<sub>5</sub>, and P<sub>6</sub> due to the three component traits while negative effects for P<sub>8</sub>, P<sub>9</sub>, P<sub>11</sub>–P<sub>13</sub>, P<sub>17</sub>–P<sub>19</sub> due to these three component traits.

Although boll weight alone played no role on lint yield in terms of additive effects, the combination of this trait with boll number accounted for the majority of additive variance for lint yield. This indicated that selection of high yielding pure lines needs consideration of both boll weight and boll number.

#### *Dominance contribution effects*

Our previous study showed that the dominance effects were a primary genetic factor responsible for

lint yield (McCarty et al. 2004a). The size of heterosis of a cross is determined by homozygous dominance effects of two parental lines and heterozygous dominance effect of that cross. Detection of dominance contribution effects may help breeders determine heterosis of a target trait (lint yield in this study) related to the dominance effects of one or several component traits.

The correlations between predicted dominance effects for lint yield and dominance contribution effects to lint yield were estimated. Except that the correlation coefficients were not significant between dominance effects for lint yield and the dominance contribution effects, the dominance effects for lint yield had significant and positive correlations with dominance contribution effects due to each single component trait or each combination of multiple component traits (Table 4). The results showed that the squared correlation coefficients were close to the dominance contribution ratios, indicating the consistence of estimation of dominance contribution ratios (Table 2) and prediction of dominance contribution effects (Table 4).

Numerically, 18 out of 19 homozygous dominance effects on lint yield were negative, while 50 out 70 crosses had positive heterozygous dominance effects

on lint yield, indicating that the majority of these crosses should have positive heterosis for lint yield (Table 4).

As we previously stated that the dominance variance in lint yield was mainly accounted for by boll number or boll number with other component trait(s) (Table 2), predicted dominance contribution effects affirmed this pattern. Generally, the contribution effects on lint yield due to boll number, or boll number with other component trait(s) were close to the dominance effects for lint yield. For example, lower homozygous dominance effects for parents 3, 6, 9, 13, 14, 17 and heterozygous dominance effects for crosses  $1 \times 10$  and  $2 \times 19$  were related to lower homozygous dominance contribution effects due to boll number, or boll number with other component trait(s). Positive heterozygous dominance effects on lint yield for crosses  $1 \times 6$ ,  $2 \times 8$ ,  $2 \times 9$ ,  $3 \times 17$ ,  $5 \times 6$ , and  $5 \times 14$  were related to the corresponding contribution effects due to boll number or boll number with other component trait(s).

Although boll weight or lint percentage alone played a small role in determining dominance effects on lint yield (Table 2), some dominance effects (both homozygous and heterozygous) for lint yield were significantly contributed by lint percentage or boll weight alone. For example, homozygous dominance effects for parents 6, 8, 10, 11, 12, 13, 14, 17, and 18 and heterozygous dominance effects for crosses  $1 \times 6$ ,  $1 \times 18$ ,  $3 \times 12$ , and  $5 \times 6$  were significantly related to lint percentage. Homozygous dominance effect for parents 4 and 13 and heterozygous dominance effects for crosses  $1 \times 8$ ,  $2 \times 13$ , and  $3 \times 12$  were significantly related to boll weight.

In some cases, a single trait alone made non-significant dominance effect contributions to lint yield; however, the combination of two traits made significant dominance contribution effects to lint yield. For example, no boll weight or boll number made a significant homozygous dominance effect contributed to lint yield for parents 8 and 10; however, combination of boll weight and boll number made significant dominance contribution effects to lint yield for these two parents ( $-220.9$  kg/ha and  $-171.4$  kg/ha, respectively). Similar examples were found for crosses  $1 \times 11$  and  $1 \times 18$ . The results suggested the importance of considering both traits used for hybrid yield improvement.

### AA contribution effects

Our previous study showed that the AA effects were one of the more important genetic factors controlling lint yield (McCarty et al. 2004a, b). AA effects are not only responsible for determining heterosis (Xu and Zhu 1999) but also useful for pure line selection because AA effects can be fixed through selection. Thus detecting AA contribution effects is very useful for a target trait (lint yield in this study) improvement through indirect selection of one or several component traits.

The correlations between predicted AA effects on lint yield and predicted AA contribution effects to lint yield were estimated. The results showed that AA effects on lint yield had significant and positive correlations with AA contribution effects due to each single component trait (except lint percentage) and multiple component traits (Table 5). The results showed that the squared correlation coefficients were very close to the AA contribution ratios.

In the same way as dominance contribution effects, AA contribution effects can be classified as homozygous and heterozygous. The patterns of AA contribution effects from component traits to lint yield were different among parents. For example, the homozygous AA contribution effects on lint yield were  $-34.6$  kg/ha,  $-46$  kg/ha,  $-45.4$  kg/ha, and  $-60.9$  kg/ha were due to lint percentage, lint percentage with boll weight, lint percentage with boll number, and lint percentage with boll number and weight for parent 6, respectively (Table 5). It appeared that lint percentage or lint percentage with other component traits, boll weight and/or boll number was an important contributor to homozygous AA effect for this parent. Another example was that no single component trait made significant AA contribution effect to lint yield for parent 11, while each of component trait combinations had significant AA contribution effects to lint yield (lint percentage with boll weight,  $-36.5$  kg/ha; lint percentage and boll number,  $-51.2$  kg/ha; boll weight and boll number,  $-54.5$  kg/ha, and three component traits,  $-62.8$  kg/ha, respectively). In some cases, no single component trait made significant AA contribution effect to lint yield, while parts of combinations of these traits made significant AA contribution to lint yield, i.e. parents 13 and 19 and crosses  $2 \times 6$ ,  $5 \times 15$ , and  $5 \times 16$ . The above results

suggested that yield component traits used for yield improvement could be genotype-specific.

## Discussion

Among many types of epistatic effects, AA effects may be the most attractive for plant breeding. AA effects can be used for pure line selection because they can be fixed since additive effects are fixable (McCarty et al. 2004a). In addition, AA effects can be classified as homozygous and heterozygous, thus they can be used to predict heterosis for a specific cross as dominance effects (Xu and Zhu 1999; McCarty et al. 2004b). In this study, we applied the ADAA genetic model with the conditional approach extended from our previous study (Wu et al. 2004, 2006a).

Phenotypically, boll number was the major contributor to lint yield. Similar results were also reported in our previous studies (Wu et al. 2004, 2006a) and other studies (Zhu 1995; Wen and Zhu 2005). Therefore, boll number is a determining component trait for cotton lint yield. As found in this study and other studies (Wu et al. 2004, 2006a), boll weight alone was not an important component trait for cotton lint yield in terms of various types of genetic effects; however, the combination of this trait with boll number greatly improved the contributions to lint yield compared to boll number or boll weight alone. For example, the contribution ratios for additive effects, dominance effects, and AA effects due to boll weight were 0%, 6.4%, and 24%, respectively and those due to boll number were 50.3%, 85.6%, and 80.4%, respectively (Table 2). However, the corresponding contribution ratios due to boll number and boll weight became 85.9%, 100%, and 91.8%, respectively. Similar results were also found in predicted contribution effects. Therefore, the heterosis and genotypic values in lint yield should be highly related to these contribution effects due to boll number and boll weight. The above results suggested that an appropriate breeding scheme with balanced selection for boll number and boll weight is very important for cotton yield improvement.

Yield and fiber strength are two important traits to be improved in current cotton breeding programs. The day-neutral lines used in our previous studies (McCarty et al. 2004a, b) and this study were selected for high fiber strength during their development.

These lines were used as male parents to cross to five commercial cultivars. The correlation between lint yield and fiber strength was  $-0.71$  and  $-0.33$  for additive effects for AA effects (these effects were calculated by McCarty et al. 2004b). However, since both additive effects and dominance effects had small contributions to lint yield (6.1% and 3.0%, respectively), the negative correlations between these two traits regarding additive effects and AA effects should not have major determining influence on the phenotypic correlation between these two important traits. That's why most  $F_6$  hybrids had no significant difference in lint yield from the commercial parents while they were significantly greater than their corresponding female parents (commercial parents) for fiber strength (McCarty et al. 2004b). Therefore, high yielding lines or hybrids with improved fiber quality could be obtained through a balanced selection of boll number and boll weight from some hybrids.

The phenotypic contribution ratios obtained by the conditional approach are equivalent to the coefficients of determination obtained by linear regression analysis (Wu et al. 2004). Thus, the conditional approach applied to dissect the genetic relationship between a complex trait and its component traits has advantages over the regression analysis in three aspects: (1) contribution ratios regarding different types of genetic effects can be determined; (2) different types of genetic contribution effects, i.e. additive or AA contribution effects in this study, can be determined; and (3) the genetic model is expandable.

The materials used in our two previous studies (Wu et al. 2004, 2006a) and in this study were different. For example, the materials used in Wu et al.'s study (Wu et al. 2004) were two parental lines and 188 recombinant inbred lines derived from these two parents. Eleven commercial cultivars were used in another study (Wu et al. 2006a). In this study, the materials we used were 14-day-neutral lines developed from race stocks (McCarty et al. 2004a), five commercial cultivars, and their  $F_2$  hybrids. In addition, the genetic model used in the two previous studies differed from the one used in this study. However, the phenotypic contribution ratios obtained by this study (bottom line of Table 2) and the two previous studies (bottom line of Table 4, Wu et al. 2004) and (bottom lines of Table 2, Wu et al. 2006a) were very comparable. Thus, the results suggest that



genetic relationships between lint yield and its component traits could be different while phenotypic relationships between yield and its component traits appear similar. Boll number used in this study and one previous study (Wu et al. 2004) were calculated by seed cotton yield and boll weight determined by sampled bolls from the middle part of plants (Tang et al. 1996), while boll number and boll weight used in the other study (Wu et al. 2006a) was determined from box mapping data. Thus, the results suggest that boll number calculated by harvested seed yield and hand-harvest boll samples is comparable to box mapping data (Jenkins and McCarty 1995), which is very time-consuming. In addition, it appears that boll weight determined by hand-harvest boll samples from the middle of plants is a good representative to boll weight from the whole plants.

Genotype by environment interaction is an important character for a quantitative trait. Thus, a genetic experiment is usually conducted over multiple environments. The environmental effects can be considered as fixed (Zhu 1994; Wu et al. 2003; McCarty et al. 2004a) or random (Wu et al. 2006a). The number of environments used usually is small and thus it is considered as fixed. However, environmental effects were considered random in detecting of conditional variance components and conditional effects (Wu et al. 2004, 2006a). In our previous study, the environmental effects were treated as fixed effects; while in this study of conditional analyses, we treated the environmental effects as random. Not only were the estimated variance components similar, but also were the predicted additive effects, dominance effects, AA effects obtained by both assumptions very similar (McCarty et al. 2004b). Even though we have not theoretically compared the results for these two assumptions, we would expect similar results in most cases. We plan a future investigation to further target this conclusion through a Monte Carlo simulation technique.

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